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energy;" on the contrary, our analysis, in which the quantities  $\frac{\partial r}{\partial q}$  play a significant rôle, lends little support to Helm's view regarding the physical dimensions of economic value. Such value, or, to use more exact terms, "marginal utility," does not, in the analysis here presented, appear as the intensity factor of an energy.

<sup>1</sup> Papers from the Department of Biometry and Vital Statistics, School of Hygiene and Public Health, Johns Hopkins University, No. 40.

<sup>2</sup> Helm, G., *Die Lehre von der Energie*, Leipsic, 1887, pp. 72 et seq.

<sup>3</sup> Ostwald, W., *Energetische Grundlagen der Kulturwissenschaften*, Leipsic, 1909, p. 155. *Die Philosophie der Werte*, Leipsic, 1913, pp. 260, 314-317, 326, 328. Among other writers who touch on the subject of the relation of economic value and price to energy are: Budde, *Energie und Recht*, Leipsic, 1902, p. 56; Winiarski, "Essay sur la Mécanique Sociale," *Revue Philosophique*, 1900, vol. 49, p. 113. See also J. Davidson, *Qu. J. Economics*, Aug., 1919, p. 717.

<sup>4</sup> And for others whose pains and pleasures he makes his own.

## THE BEHAVIOR OF HOMOLOGOUS CHROMOSOMES IN A TRIPLOID CANNA

By JOHN BELLING

STATION FOR EXPERIMENTAL EVOLUTION, COLD SPRING HARBOR

Communicated by C. B. Davenport, June 12, 1921

In a diploid flowering plant we may regard the chromosome group as consisting of a number of sets of chromosomes, two in each set. When, there are differences of size in the group, as has been shown in *Yucca*,<sup>4</sup> *Crepis*,<sup>6</sup> *Morus*,<sup>5</sup> *Datura*, and two dozen or more other species,<sup>8</sup> the two chromosomes of each set are of the same size; they form bivalents distinguishable by their sizes at the first maturation divisions of the pollen-mother-cells;<sup>1</sup> and they can consequently be seen to replace one another in the haploid groups of chromosomes of the microspores and megaspores. Evidence from breeding, especially in cases of non-disjunction, also shows conclusively that the chromosomes of one pair are nearly equivalent or homologous.<sup>7</sup> We may then define a diploid plant, in the strict sense, as one having a chromosome group formed of pairs of homologous chromosomes. A triploid plant possibly comes either from the cross of a tetraploid and a diploid, or from the union of a normal germ-cell with a pollen-grain or egg-cell in which one of the cytoplasmic divisions of maturation has been omitted. (I have found one cytoplasmic division commonly omitted, especially after cold, in the pollen of *Stizolobium*, *Datura*, etc.) The differences in size in the chromosomes of a triploid mulberry,<sup>7,8</sup> and of a triploid *Datura*, show that the sets consist of three similar chromosomes each. The breeding results with plants in which one set consists of three chromosomes, while the other sets have only two, show

that the three are homologous.<sup>2</sup> Hence we may define a triploid plant, in the strict sense, as one having a chromosome group made up of a number of sets of three homologous chromosomes.

In diploid plants there is an attraction of some kind between the two homologous chromosomes which form a bivalent or dyad at the first division. We may expect an attraction also between the three homologous chromosomes in the corresponding triploid plants, leading to the

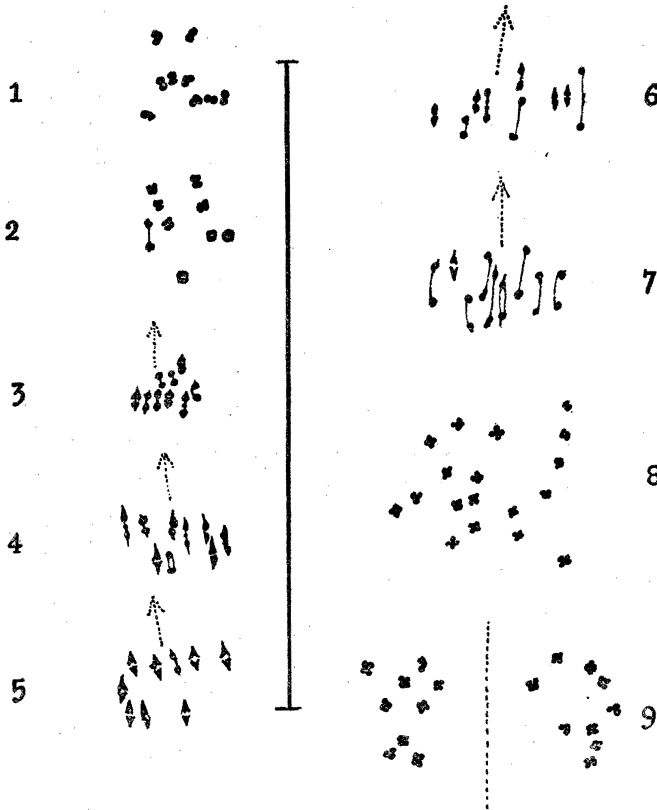


FIG 1

The drawings were made at stage height, with the Abbe camera. A Leitz 2 mm. apochromatic objective of 1.3 aperture, and compensating ocular 6 were used. An achromatic condenser of 0.9 aperture was focussed on the object so as to give critical illumination. The pollen-mother-cells were fixed and stained with iron-aceto-carmin (1).

The assortment of the chromosomes in the pollen-mother-cells of a diploid *Canna* clone. This was obtained under the name "Madame Crozy." (1) Prophase of the first division, showing 9 bivalents. (2) Metaphase of the first division, showing 9 dyads, one already divided. (3), (4), (5), (6), and (7) are stages of early anaphase, showing division of the 9 dyads into 9 + 9 chromosomes. (The arrows indicate the situation of the polar axis.) (8) After the first division, showing 18 chromosomes. (9) The two groups in the metaphase of second division, separated by a cell-wall.

formation of triads. Thus Wilson<sup>9</sup> observed that three small chromosomes in *Metapodium* were grouped into a triad in the first division, and separated so that two went to one pole and one to the other. Osawa<sup>5</sup> found in triploid mulberries that some of the single chromosomes might be attached to the dyads in the first division of the pollen-mother-cells. In one triploid *Canna* (and in a triploid *Datura*), however, I found that all the chromosomes regularly form triads in the prophase and metaphase of the first division, and pass, two and one, in a random manner, to either pole.

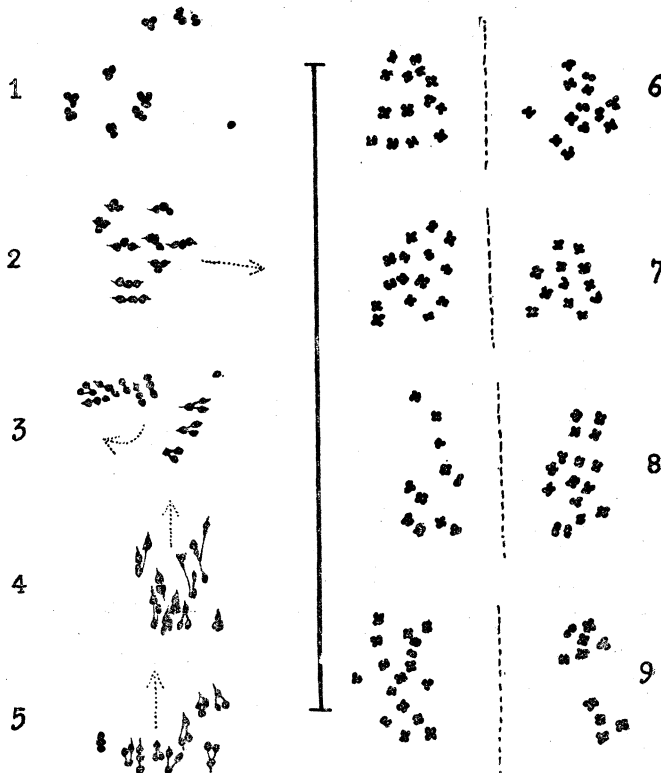


FIG. 2

The assortment of the chromosomes in the pollen-mother-cells of a triploid *Canna*.

(1) Prophase showing triads. One chromosome separated from its corresponding dyad. (2), (3), (4), and (5) metaphase and early anaphase groups. In (3), one chromosome has again separated from its two partners. (6), (7), (8), and (9) metaphase plates for the second divisions, with cell-wall between, showing, respectively, 14 + 13, 15 + 12, 11 + 16, and 17 + 10 chromosomes.

In 1920 I grew 46 differently named clones and species of *Canna*, obtained, without particular selection, from three leading dealers of New York, Philadelphia, and Florida, and from the U. S. Department of Agriculture. The chromosomes of 31 of these were counted in the first or second divisions of the pollen-mother cells; about 250 groups being

drawn with the camera. Of these 31 clones, 22 showed nine dyads or bivalents, which split into  $9 + 9$  at the first division (fig. 1); 3 clones had a total of 18 single chromosomes (or 9 bivalents), which divided at the first division into  $8 + 10$ , or other unequal numbers, not commonly into  $9 + 9$ ; 5 clones were probably completely or nearly triploid, and irregular in their first division, resembling in this the triploid mulberries of Osawa,<sup>5</sup> and like them showing a smaller number of chromosomes after the first division than the triple number (in these cases, 24 to 26 instead of 27); while one clone was regularly triploid, showing nine triads at the prophase and first metaphase, and a total of 27 chromosomes after the first division.

This regularly triploid clone was obtained from Thorburn, New York, in 1920, under the name "Gladiator." It differed conspicuously from other Cannas with more than 18 single chromosomes, in its smaller flowers and lesser size, resembling in these the ordinary diploid Cannas. Thirty-two pollen-mother-cells were drawn with the camera. In 18 of these pollen-mother-cells, the total number of chromosomes could be accurately counted, and was 27. In the 3 other cases where the total number could be counted, some chromosomes seemed to be missing, for the totals were 25, 25, and 24. (In 3 pollen-mother-cells showing the anaphase of the first division, or the metaphase of the second, only one group could be accurately counted, because of the slanting position of the other. In the 8 remaining prophase or metaphase figures, not all the trivalent chromosomes could be distinguished from the bivalents or univalents into which they had divided, or from which they were composed.)

Nine of the cells showed clearly how many chromosomes went to one pole and how many to the other after the first division.

Chromosome partition	$18 + 9$	$17 + 10$	$16 + 11$	$15 + 12$	$14 + 13$
Nos. of cells found	0	1	2	2	4
Calculated on random distribution	0.04	0.3	1.3	3.0	4.4

(In the triploid *Datura* the chromosomes have been accurately counted in 64 pollen-mother-cells after the first division, and the distribution corresponds with a random one.)

Three of the early anaphase plates showed how the triads divided. Taking for "up" the upper side of the camera drawing, which was a random position, we have for the position of the two's with regard to the equator (fig. 2, Nos. 4 and 5):

	Up	Down	Doubtful
Third pollen-mother-cell	4	4	1
Second pollen-mother-cell	4	3	2
First pollen-mother-cell	2	4	3
Totals	10	11	

In several prophases, one chromosome was disconnected from its corresponding dyad (fig. 2, Nos. 1 and 3). If this occurred more frequently it would lead to the condition found in the large-flowered Cannas, where triads, dyads, and monads are mingled at the metaphase; or to the situation of Osawa's mulberry clones, where triads are apparently less common; or finally to the triploid *Oenothera lamarckiana*, which, according to Geerts,<sup>3</sup> shows only dyads and monads. In the triploid Canna, one complete count of both second divisions was made in a pollen-mother-cell. On one side of the cell-wall the numbers were 15 + 1 + 12, and on the other side, 13 + 13. The single chromosome seemed attached to the cell-wall.

About half of the pollen-grains of this triploid Canna were nearly or quite empty; while the others were full or nearly full of cytoplasm, with one or more nuclei.

*Summary.*—(1) Most of the Cannas examined were diploid, showing nine dyads before the first division in the pollen-mother-cells, and these in most plants separated into 9 + 9.

(2) One of the triploid Cannas showed commonly nine triads, each of which separated into two and one on the spindle, in a random manner with regard to the two poles. (The same arrangement, though less easy to demonstrate, was also found in a triploid *Datura*.)

<sup>1</sup> Belling, J., 1921, "On Counting Chromosomes in Pollen-Mother-Cells," *Am. Nat.*

<sup>2</sup> Blakeslee, A. F., J. Belling, and M. E. Farnham, 1920, "Chromosomal Duplication and Mendelian Phenomena in *Datura* Mutants," *Science*, **52**, 388-390.

<sup>3</sup> Geerts, J. M., 1911, "Cytologische Untersuchungen einiger Bastarde von *Oenothera gigas*," *Ber. Deutsch. Bot. Ges.*, **29**, 160-166.

<sup>4</sup> Müller, C., 1910, "Über karyokinetische Bilder in den Wurzelspitzen von *Yucca*," *Pringsh. Jahrb. wiss. Bot.*, **47**, 99-117.

<sup>5</sup> Osawa, I., 1920, "Cytological and Experimental Studies in *Morus*, with Special Reference to Triploid Mutants," *Bul. Imp. Sericult. Exp. Sta. Japan*, **1**, 317-369.

<sup>6</sup> Rosenberg, O., 1918, "Chromosomenzahlen und Chromosomendimensionen in der Gattung *Crepis*," *Arkiv Botanik*, **15**, No. 11, pp. 1-16.

<sup>7</sup> Tahara, M., 1910, "Über die Kernteilung bei *Morus*," *Bot. Mag. Tokyo*, **24**, 281-289.

<sup>8</sup> Tischler, G., 1915, "Chromosomenzahl-, Form, und-Individualität im Pflanzenreiche," *Prog. Rei. Bot.*, **5**, 164-284.

<sup>9</sup> Wilson, E. B., 1910, "Studies on Chromosomes VI. A New Type of Chromosome combination in *Metapodium*," *J. Exp. Zool.*, **9**, 53-78.